

3D diving behavior of Weddell seals with respect to prey accessibility and abundance

Yoko Mitani^{1,4,*}, Yuuki Watanabe³, Katsufumi Sato^{1,5}, Michael F. Cameron^{2,6},
Yasuhiko Naito¹

¹National Institute of Polar Research, 1-9-10 Kaga, Itabashi, Tokyo 173-8515, Japan

²University of Minnesota, 100 Ecology, St. Paul, Minnesota 55455, USA

³Center for International Cooperation, Ocean Research Institute, The University of Tokyo, 1-15-1 Minamidai, Nakano, Tokyo 164-8639, Japan

⁴Present address: Department of Marine Biology, Texas A&M University at Galveston, 5007 Avenue U, Galveston, Texas 77551, USA

⁵Present address: International Coastal Research Center, The Ocean Research Institute, The University of Tokyo, 2-106-1 Akahama, Otsuchi, Iwate 028-1102, Japan

⁶Present address: National Marine Mammal Laboratory/NOAA, 7600 Sand Point Way NE, Seattle, Washington 98115, USA

ABSTRACT: The foraging behavior of predators is influenced by the distribution of prey at different spatial and temporal scales. In marine environments, aquatic animals move in 3 spatial dimensions; however, previous studies of the fine-scale movements of predators were limited to only the vertical component of diving behavior. Here, we have analyzed image data along the 3D dive paths of Weddell seals *Leptonychotes weddellii* to address the 3D nature of their interactions with prey at the spatial and temporal scales relevant to an individual predator. The 3D dive paths were calculated using acceleration and geomagnetic intensity data. A prey index was estimated using image data taken by digital still picture loggers. The descent and ascent phases of a dive were more linear than the bottom phase, and the prey index during the bottom phase was significantly higher than those during the descent and ascent phases. These results suggest that the bottom phase does indeed represent time spent foraging in a prey patch, and that the descent and ascent phases represent the transit between an ice hole and a prey patch. The 3D dive paths of individual seals were affected by the location of breathing holes in the ice and by the slope of local bathymetric features around their breeding colony. Our data suggest that once seals encounter prey, they dive no further, which minimizes their distance from the breathing hole and maximizes their time spent foraging.

KEY WORDS: Foraging behavior · 3D dive paths · Prey distribution · Prey availability · Weddell seal · *Leptonychotes weddellii*

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INTRODUCTION

Quantitative studies of predator–prey interactions depend on knowledge of their spatial dynamics and behavior. Studies in marine environments are limited by our inability to comprehensively assess an animal's behavior beneath the water. The recent development and use of animal-borne cameras with time-depth recorders allow researchers to better understand the foraging behavior of predators in rela-

tion to their environment (Davis et al. 1999, Ponganis et al. 2000, Fuiman et al. 2002, Hooker et al. 2002, Sato et al. 2002, Watanabe et al. 2003). Diving animals forage in vertical as well as horizontal dimensions in marine environments (Zamon et al. 1996, Davis et al. 1999, Simpkins et al. 2001, Hindell et al. 2002). However, except for a small number of studies that link predator movement with prey distribution (Davis et al. 1999, 2003), most research has been limited to only 2 dimensions, time and depth. More

*Email: mitaniy@tamug.edu

recently, the underwater feeding behaviors of seals have been described in detail with the reconstruction of 3D dive paths (Davis et al. 1999, 2003, Simpkins et al. 2001, Hindell et al. 2002, Mitani et al. 2003). In this study, we combine image data and 3D movements to address the 3D nature of the interactions between Weddell seals *Leptonychotes weddellii* and their prey under sea ice.

Weddell seals haul out annually along cracks in the sea ice during the breeding season (October to December), to rest, give birth and nurse their pups. Some of these females spend considerable time performing deep dives, where they have been shown to encounter prey (Sato et al. 2002). These dives suggest that supplemental foraging trips during the lactation period may be an important maternal reproductive strategy for female Weddell seals (Sato et al. 2002). Weddell seals foraging beneath the extensive fast ice are tied not only to the sea surface, but also to their breathing hole. Testa et al. (1989) showed that the efficiency of weight transfer to pups was not related to the number of dives, suggesting that factors other than the number of dives, such as prey accessibility or abundance, may have been responsible for differences in foraging success. To quantify how differences in foraging behaviors are related to prey availability and the physical environment, 3D dive profiles and prey abundance information were collected simultaneously from Weddell seals in McMurdo Sound, Antarctica. The fine-scale 3D paths were reconstructed using a method described by Mitani et al. (2003) and we used the local prey abundance information reported by Watanabe et al. (2003). The aim of this study was to describe an individual's prey accessibility in relation to its physical surroundings and examine whether 3D dive paths were related to 3D prey distribution.

MATERIALS AND METHODS

Field experiments. Experiments were conducted on lactating Weddell seal females with live pups from November 24 to December 10, 2000, at Big Razorback Island (77.68°S, 166.50°E) and Turks Head (77.67°S, 166.78°E) in the region of McMurdo Sound, Ross Island, Antarctica. Both breeding sites are covered by fast ice during the breeding season. Tidal cracks or holes drilled through the sea ice facilitated the use of a depth gauge (type-8, Tsurumi Seiki) to measure the bathymetry of each study site. At Big Razorback Island, these cracks are oriented close and parallel to the coastline of the island. As such, to reach deep water quickly, seals must swim at a relatively shallow angle (approx. 30°) and follow the slope of the island (Fig. 1a). In contrast, the primary crack at Turks Head is perpendicular

to the coastline and over deep water. Additionally, the underwater slope is much steeper than at Big Razorback Island, and seals along this crack may dive steeply to reach deeper depths (Fig. 1b).

The females were anesthetized using the inhalant Sevoflurane (Kusagaya & Sato 2001). A quick-setting epoxy resin (Evercoat Ten-Set; Fibre Grass-Evercoat) was used to attach 3 types of data loggers (acceleration data loggers, D2GT, geomagnetic data loggers, 3MPDT and digital still camera loggers, DSL) to their dorsal pelage. The data loggers were attached to 2 seals at Big Razorback Island and to 3 seals at Turks Head, and were retrieved 2 or 3 d later. The remaining adhesive fell off with the pelage at molt.

3D dive data analysis. 3D dive paths were calculated using acceleration and geomagnetic intensity data, as described in detail in Mitani et al. (2003). The acceleration and geomagnetic intensity data were collected by 2 instruments (i.e. D2GT and 3MPDT) attached to each seal. The D2GT (W1000L-D2GT: 23 mm diameter, 90 mm length, 70 g in air; Little Leonardo) recorded 2-axes acceleration at intervals of 1/16 s, depth at 1 s intervals and temperature every 30 s. The second device, a 3MPDT (W380TL-3MPDT: 24 mm diameter, 189 mm length, 120 g in air; Little Leonardo), recorded changes in 3D geomagnetic intensity at 1 s intervals. The 3MPDT also recorded depth, rotations of a propeller per second (rps) at 1 s intervals and temperature every 30 s. Following Sato et al. (2003), we used rps to estimate swimming speed by creating a calibration line from a linear regression of rps against a second independent method of calculating swimming speed based on body angle (from an acceleration sensor along the longitudinal axis of the seal) and vertical speed (as determined from the depth recorder). The seals' body angle and posture were calculated from the acceleration data and the heading from the geomagnetic intensity data. Together with swim speed, the seals' 3D underwater dive paths were reconstructed for each dive.

For the analyses presented here, we only used dives with a maximum depth greater than 200 m, which were classified as hunting dives by Kooyman (1968). Each dive was subdivided into a descent phase (from the beginning of a dive to the time of the first ascent while deeper than 50 m deep), an ascent phase (from the depth of the last descent while deeper than 50 m to the end of dive) and a bottom phase (the time between the end of descent and beginning of ascent). Dive data were analyzed to determine diving efficiency (bottom time/[dive duration + post-dive interval]; excluding the last dive in a bout; Kooyman & Kooyman 1995). In addition to these equations, we calculated an index of path straightness for each phase of a dive as the straight-line distance between the starting and ending points divided by the actual length of the path traveled.

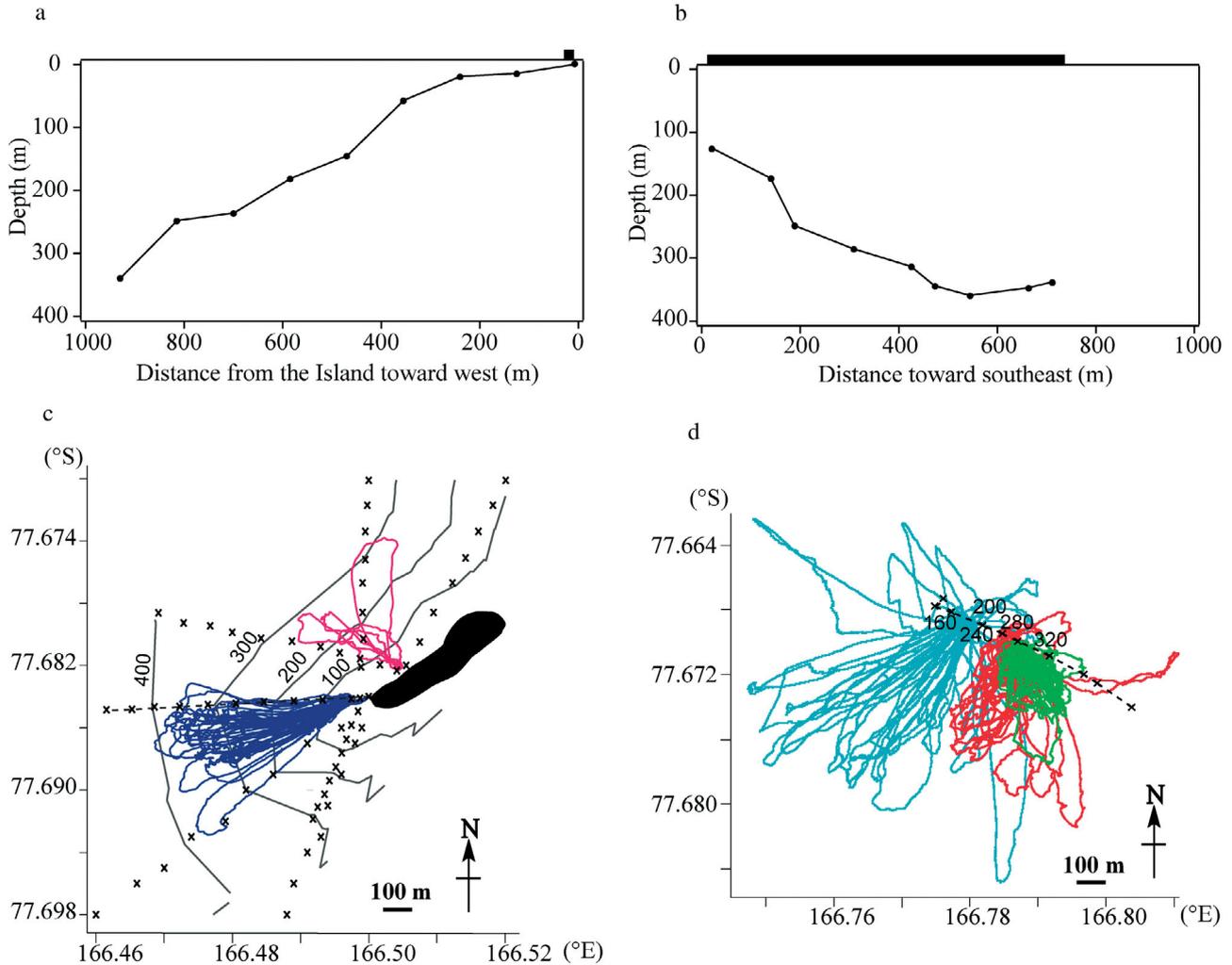


Fig. 1. Bathymetric diagram of (a) Big Razorback Island and (b) Turks Head. The location of ice holes and tidal cracks are shown by black horizontal bars. The dive paths of each seal in relation to the bathymetry around (c) Big Razorback Island and (d) Turks Head. Each seal is represented by a different color and 'x' indicates the location of a depth gauge measurement

Image data analysis. A prey index was estimated using a third device, a DSL (DSL-1000DV: 3.4 kg in air [approximately 1% of a seal's body mass] and 1.6 kg in water; Little Leonardo), which provided the underwater still images, described in detail in Watanabe et al. (2003). The camera was pressure-resistant to a depth of 2000 m. The DSL was composed of 2 cylindrical housings, each 230 mm in length and 52 mm in diameter. One housing contained the color digital camera and the other housing contained a flash. In complete darkness, the onboard microcomputer synchronized the flash and camera, and maintained a pre-programmed sampling interval of 30 s and a pressure-sensed depth threshold of 5 m. The camera was able to store approximately 700 images and recorded depth data at 1 s intervals. Prey objects of each image were digitally isolated, identified and counted using image processing software (Win-

ROOF Version 3.53; Mitani) and prey index was defined as: $\text{Prey index} = (A_o/A_a) \times (n \times A_w/A_a)$, where A_o = total area occupied by objects, A_a = available area which excluded the area of the other data logger, n = number of objects and A_w = whole area of the image (Watanabe et al. 2003). Prey indices were compared between the bottom phase and the transit phase (descent phase + ascent phase).

Using the 3D dive paths, we calculated the straight-line distance from the breathing hole to the point where an image i was taken (the straight-line distance, $\text{SLD}(i)$) and the farthest point attained (the maximum straight-line distance, SLD_{MAX}). We expected SLD_{MAX} to differ between dives in relation to where seals encountered prey. The difference between these 2 statistics, termed the aligned distance (aligned distance, $\text{AD}(i)$), described how far from the SLD_{MAX} the seals

encountered prey for each dive: $AD(i) = -[SLD_{MAX} - SLD(i)]$. Therefore, for an image i taken at the farthest point from the breathing hole [$SLD(i) = SLD_{MAX}$], the $AD(i)$ would be 0. Results are presented as means \pm SD.

RESULTS

Each seal at Big Razorback Island dived perpendicularly across bathymetric lines (Fig. 1c) to reach deep water, while the 3 seals at Turks Head primarily dived to the south, away from land to the north (Fig. 1d). Fig. 2 shows typical examples of reconstructed 3D dive paths and prey index. 'Marilyn', at Big Razorback Island, followed the bathymetric slope of the island to reach deeper water (Fig. 2a). In contrast, 'Madonna', at Turks Head, dived with a steeper dive angle to reach the bottom (Fig. 2b). The diving efficiency of Big Razorback Island seals (0.37 ± 0.12 , median = 0.37, $n = 26$) was significantly lower than Turks Head seals (0.46 ± 0.09 , median = 0.47, $n = 81$; Mann-Whitney U -test, $p < 0.0005$). The index of path straightness calculated for the bottom phase of each seal was less linear than in the descent and ascent phases (Scheffé's test, $p < 0.0001$, Table 1).

For dives with a maximum depth deeper than 200 m, the DSLs provided 423 images for the 11 dives at Big

Razorback Island and 1020 images for the 28 dives at Turks Head (Table 2). There was no significant difference in prey index at the bottom phase between Big Razorback Island and Turks Head (0.13 ± 0.33 for Big Razorback Island and 0.15 ± 0.94 for Turks Head, Mann-Whitney U -test, $p = 0.42$). The prey index was significantly higher during the bottom phase than during the transit phase (0.08 ± 0.40 , Mann-Whitney U -test, $p < 0.005$ for Big Razorback Island; 0.02 ± 0.07 , Mann-Whitney U -test, $p < 0.0001$ for Turks Head).

The maximum horizontal distance during the bottom phase of seals at Big Razorback Island increased with an increase in maximum depth (Spearman rank correlation = 0.942, $p < 0.0001$, Fig. 3). In contrast, there was a negative correlation between these statistics at Turks Head (Spearman rank correlation = -0.406 , $p < 0.0005$). The frequency distribution of the SLD_{MAX} of DSL analyzed dives was summed for each site (Fig. 4a,b). The SLD_{MAX} ranges (300 to 800 m) were similar at both sites, with a mode between 500 and 600 m for seals at Big Razorback Island and between 300 and 400 m for seals at Turks Head. The prey distribution during the bottom phase, as estimated from the images, was different between the 2 sites (Fig. 4c,d). At Big Razorback Island, there was a significant positive relationship between prey index and SLD (Spearman rank correlation = 0.248, $p < 0.0005$). At Turks Head, by contrast, prey index was not associated with

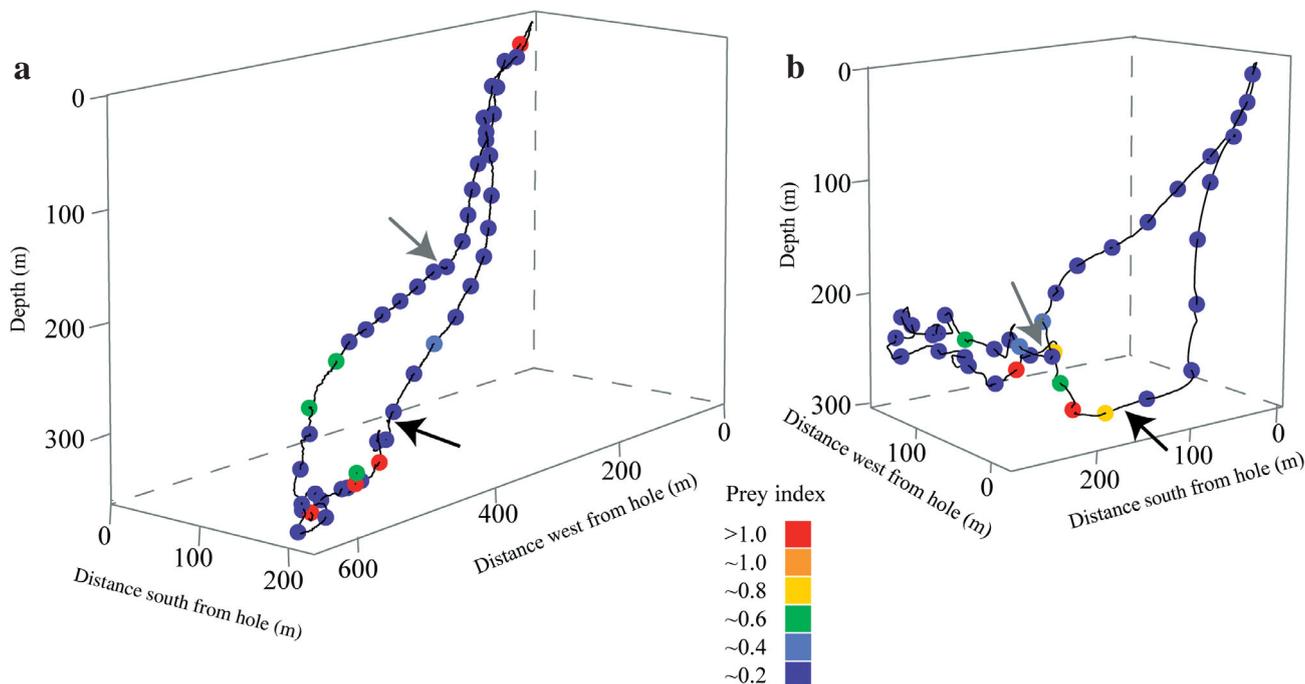


Fig. 2. Examples of reconstructed 3D dive paths of Weddell seals and prey index values. Circles on the dive paths represent the moment when an image was taken. The color of the circle represents the prey index (red for high values and purple for low values). Arrows represent the end of descent (black) and the start of ascent (gray). (a) 'Marilyn' at Big Razorback Island, with a gradual slope; (b) 'Madonna' at Turks Head, with a steeper slope

an increment in SLD (Spearman rank correlation = 0.008, $p = 0.84$). Yet when prey index of each dive was plotted against AD, the pattern of prey distribution was similar at both colonies (Fig. 5). The higher prey-index values in each dive were observed at the farther distance from the breathing hole ($AD > -100$ m).

DISCUSSION

This study shows that the foraging behavior of Weddell seals based on 3D movements is influenced by environmental characteristics, such as bathymetric features and 3D distribution of prey. According to the present study, the descent and ascent phases were more linear than the bottom phase of a dive, and the prey index at the bottom phase was significantly higher than the descent and ascent phases (Tables 1 & 2). This supports previous assumptions that the bottom phase indeed represents time spent foraging in a prey patch, and that the descent and ascent phases represent the transit between an ice hole and a prey patch (e.g. Le Boeuf et al. 1988). Although the highest prey index at Turks Head was 200 m from the breathing hole, half of the dives extended farther than 400 m from the breathing hole (Fig. 4b,d). However, this result does not indicate that seals passed through a closer prey patch. The highest prey index of each dive was observed around the maximum straight-line dis-

Table 1. Path straightness in each phase for each study site. The straightness of each dive path in the bottom phase was less linear than the descent and ascent phases. Scheffé's test, * $p < 0.0001$. Values are means \pm SD

Site	Descent	Bottom	Ascent	n
Big Razorback Island	0.95 \pm 0.30	0.28 \pm 0.15*	0.93 \pm 0.08	29
Turks Head	0.92 \pm 0.05	0.24 \pm 0.14*	0.90 \pm 0.07	81

Table 2. Digital still picture loggers (DSL) data for each breeding colony: 2 seals at Big Razorback Island and 3 seals at Turks Head. Number of images is in parentheses. Dives deeper than 200 m were used for analysis. The Mann-Whitney U-test was used. * $p < 0.005$, ** $p < 0.0001$. Values are means \pm SD

Site	No. of DSL analyzed dives	No. of DSL images	Prey index		
			Transit	Bottom	
Big Razorback Island	11	423	0.08 \pm 0.40 (203)	0.13 \pm 0.33 (220)	} NS
Turks Head	28	1020	0.02 \pm 0.07 (444)	0.15 \pm 0.94 (576)	

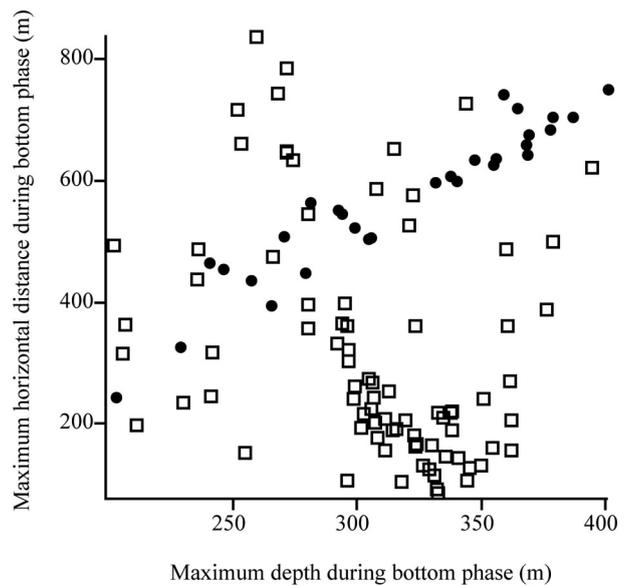


Fig. 3. Relationship between maximum depth during the bottom phase and the maximum horizontal distance during the bottom phase. (●) Dives at Big Razorback Island; (□) dives at Turks Head

tance from the breathing hole (Fig. 5). Therefore, our data suggest that once seals encounter prey, they dive no farther to minimize their distance from the breathing hole and maximize their time spent foraging. Watanabe et al. (2003) indicated that the prey *Pleurogramma antarcticum* might have a patchy distribution and that seals primarily encountered prey near the maximum depth of their dive. This study reveals that the seals' maximum dive distance is affected (and perhaps even determined) by the 3D distribution of prey. For air-breathing animals, choosing a foraging depth is an important aspect of foraging theory, as patch residence times are constrained by the requirement to return to the surface to replenish oxygen stores (Mori 1998, Thompson & Fedak 2001). Thompson &

Fedak (2001) assumed that the amount of oxygen used traveling to and from the bottom was a linear function of dive depth. But in the case of Weddell seals, which travel under extensive fields of unbroken fast ice, it is not only depth but the horizontal distance to a prey patch that is an important function, because they must return to their breathing hole.

Bathymetric variation is also likely to influence the diving behavior of individual Weddell seals. Despite the lack of a significant difference in prey abundance at the 2 colonies (Table 2), our

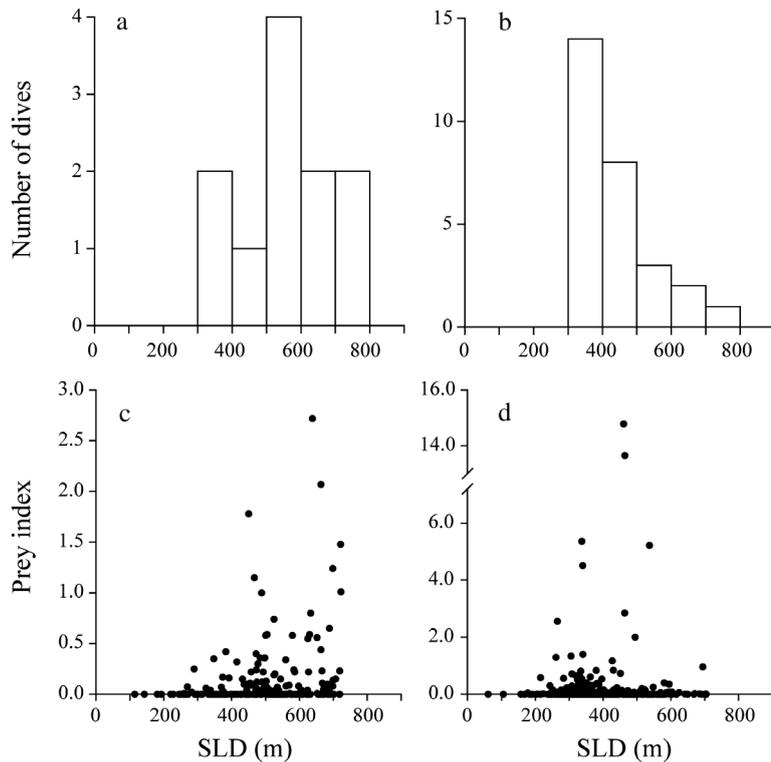


Fig. 4. Histogram of the maximum straight-line distance to the breathing hole (SLD) of DSL-analyzed dives of Weddell seals (a) at Big Razorback Island and (b) Turks Head. The relationships between prey index and the straight-line distance from the breathing hole (the straight-line distance, SLD) at (c) Big Razorback Island and (d) Turks Head. Points represent individual images

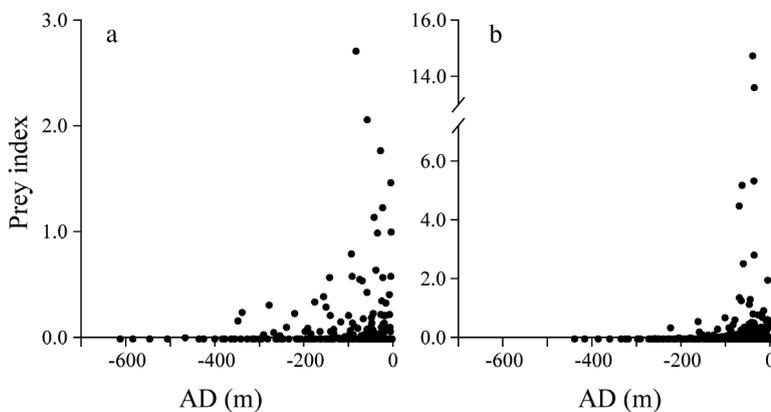


Fig. 5. Prey index in relation to the aligned distance (AD) at (a) Big Razorback Island and (b) Turks Head. Each point represents an individual image

analyses suggested that prey accessibility is lower at Big Razorback Island than at Turks Head because of the differences in underwater topography. Watanabe et al. (2003) showed the prey index at a depth of 250 to 350 m was relatively high at both sites. To reach these depths, seals at Big Razorback Island would need to travel farther than 400 m, while those at Turks Head

did not necessarily need to travel as far (Fig. 3). Seals at Big Razorback Island were restricted by the slope of the island from diving steeply to reach a prey patch (Fig. 1a). Thus, they were required to reduce the proportion of time spent foraging in order to return to the breathing hole.

Additionally, Sato et al. (2003) discovered that a steeper angle of descent facilitated gliding, which is a more energy-efficient form of locomotion than stroke swimming in Weddell seals. Indeed, all of the instrumented seals at Turks Head utilized the gliding technique to reach foraging depths, while most of the seals at Big Razorback Island were unable to glide because the island's slope prevented them from maintaining the angle necessary (Sato et al. 2003). A general prediction derived from the long-term monitoring and mark-recapture models of Weddell seals is that maternal age and experience affect offspring survival (Hastings & Testa 1998). On average, the mothers at Big Razorback are younger than those at Turks Head (M. F. Cameron, unpubl. data). Hastings & Testa (1998) suspected that the lower rate of survival of pups born at Big Razorback Island (vs Turks Head) was most likely related to colony choice of the mother, who selects for favorable pup rearing ice conditions, rather than prey availability. However, in a more recent study using time-depth and image data, Sato et al. (2002) revealed that foraging dives made during the lactation period may be an important maternal reproductive strategy for female Weddell seals. As a higher availability of prey was observed at Turks Head, where the greater aggregation of older and more experienced females rear their pups, prey accessibility may be another important component in individual pupping site choice.

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